

## Precision Grips, Hand Morphology, and Tools

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**ABSTRACT** This study asks whether there are discernable links between precision gripping, tool behaviors,<sup>1</sup> and hand morphology in modern hominoids, which may guide functional interpretation of early hominid hand morphology. Findings from a three-pronged investigation answer this question in the affirmative, as follows. (1) Experimental manufacture of early prehistoric tools provides evidence of connections between distinctive human precision grips and effective tool making. (A connection is not found between the "fine" thumb/index finger pad precision grip and early tool making.) (2) Manipulative behavior studies of chimpanzees, hamadryas baboons, and humans show that human precision grips are distinguished by the greater force with which objects may be secured by the thumb and fingers of one hand (precision pinching) and the ability to adjust the orientation of gripped objects through movements at joints distal to the wrist (precision handling). (3) Morphological studies reveal eight features distinctive of modern humans which facilitate use of these grips. Among these features are substantially larger moment arms for intrinsic muscles that stabilize the proximal thumb joints. Examination of evidence for these reveals that three of the eight features occur in *Australopithecus afarensis*, but limited thumb mobility would have compromised tool making. Also, Olduvai hand morphology strongly suggests a capacity for stone tool making. However, functional and behavioral implications of Sterkfontein and Swartkrans hand morphology are less clear. At present, no *single* skeletal feature can be safely relied upon as an indicator of distinctively human capabilities for precision gripping or tool making in fossil hominids. *Am J Phys Anthropol* 102:91-110, 1997. © 1997 Wiley-Liss, Inc.

Functional analysis of fossil hominid hands generally includes an assessment of their ability to use modern human precision grips (Napier, 1959, 1961, 1962a,b, 1993; Lewis, 1977, 1989; Susman and Creel, 1979; Susman 1988a,b, 1989, 1991, 1994; Tuttle, 1981; Marzke, 1983; Marzke and Shackley,

1986; Shrewsbury and Sonek, 1986; Brain et al., 1988; Ricklan, 1990). This ability is considered a significant element of the evolving hominid hand/brain/tool complex. Inferences drawn from fossil hand bones about the potential for precision gripping have served sometimes to establish whether or not a fossil hand was capable of both tool using and tool making (Napier, 1959; Susman, 1991). This paper points to flaws in such inferences from the Olduvai and Swartkrans fossil hand bones, and proposes the

<sup>1</sup>The term "tool behavior" has been variously used in the literature, in some cases implying exclusively tool making distinctive of humans (Susman, 1991) and in others referring variably to tool using and/or tool-making abilities, some shared with us by other animals (Susman, 1988a,b, 1994). In this paper the term is used to include both tool using and tool making behaviors of humans and non-humans; the term "tool making" is used in place of "tool behavior" whenever the discussion is focused upon distinguishing a capacity for removing flakes from stone preforms from a more general capacity to manipulate stone tools.

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use of eight morphological features to predict precision grip capabilities that facilitate habitual, effective prehistoric stone tool making. Evidence in the literature to support the use of these features rests on investigation involving (1) the experimental replication of prehistoric tools by archaeologists, (2) the comparison of three catarrhine species in manipulative behavior, and (3) the biomechanical analysis of hand and wrist morphology in chimpanzees.

The investigation asks the following: What precision grips are essential to habitual and effective manipulation of prehistoric stone tools? Are these grips shared with other catarrhine species? Are there morphological features distinctive of each species which are essential to the effective use of their respective precision grip repertoires? Is there fossil evidence for the origin and evolution of morphological features that specifically reflect precision grip capabilities, including human precision grip capabilities that facilitate effective prehistoric tool making? The answers are drawn by integrating my collaborative research results with those of other investigators. The primary goal of the paper is to bring into focus the full, integrated body of evidence for morphological adaptations to prehistoric tool making, which cannot easily be discerned in reports of the separate research projects.

#### **HISTORICAL REVIEW: THE PRECISION GRIP QUESTION**

The term "precision grip" is defined here as any grip that involves the thumb and one or more fingers, with or without the palm serving passively as a prop. It is distinguished from the term "power grip," in which objects are strongly squeezed by the fingers alone or squeezed by the fingers, thumb, and actively by the palm. The first term was introduced by Napier (1956), who defined it as one in which an object is pinched between part or the whole flexor aspect of the fingers and the opposing thumb. He related the grip to morphological facilities for abduction and medial rotation at the carpometacarpal and metacarpophalangeal thumb joints, flexion and abduction at the finger metacarpophalangeal joints, and wrist dorsiflexion mid-

way between radial and ulnar deviation. This classic paper simplified the analysis of hand postures and movements by demonstrating that these fall into two categories, one (precision grips) involving the thumb opposed to the fingers and allowing precision control of objects, and the other (power grips) incorporating the palm of the hand as well, to secure the object as an extension of the forearm for use in forceful activities such as hammering.

The "precision" term is often restricted to grips in which a small object is held between the thumb's distal phalanx and the terminal volar pads of one or more fingers. This is the type of grip specified or implied in discussions of the potential for precision gripping by fossil hominid species in several papers by Napier (1959, 1961, 1962a,b, 1964), Krantz (1960), Susman (1979, 1988a,b, 1989, 1991), and Susman and Creel (1979). My definition is considerably broader. A focus on the thumb pad/distal index pad grip restricts the amount of information on precision gripping and tool-making potential that might be gleaned from the structure of fossil hominid hand bones. Kinematic and electromyographic studies of the human hand take account of a much greater variety of thumb/finger postures and movements used in securing, holding, and maneuvering objects with precision (see, for example, Landsmeer, 1962; Long et al., 1970; Long, 1981; Chao et al., 1976, 1989). In particular, the importance of the ability to maneuver, as well as to retrieve and hold objects with precision, seems to have been almost completely ignored by physical anthropologists, with the exception of Krantz (1960). Therefore, I have adopted a definition of precision gripping that is more reflective of what the hand actually does in tool use.

Over time the discussion of precision grips became reduced in the physical anthropological literature to the claim that the potential for one type of precision grip (between the distal thumb and distal index finger pad) is linked to one aspect of hand morphology (relative thumb length) and to a capacity for stone tool making. In my view these links have not been established; no simple test in

hand morphology exists for establishing tool-making as opposed to exclusively tool-using potential in fossil hominids. In particular, Susman's (1988a,b, 1989) arguments from the morphology of *Paranthropus* to precision gripping, and from precision gripping to tool making are not supported by the criteria on which he relies, which include (1) relative thumb length (Susman, 1988a) and (2) links between Olduvai hand morphology, thumb-fingertip precision gripping, and tool making (Susman, 1988b). Evidence regarding (1) is not provided for *Paranthropus*, and Napier (1962a) largely dismissed (2) because he could not find evidence for relative thumb length in the Olduvai hand, and he was able (like Krantz, 1960) to reproduce early hominid stone tools without using the precision grip. It is regrettable that the focus on hominid hand evolution has become almost exclusively concentrated on a single type of precision gripping behavior, about which insufficient evidence is available from the fossil record, and whose importance for Oldowan tool making is not established. A larger body of evidence is evaluated below for possible links between morphology, precision gripping, and tool behaviors. A new grip classification scheme is presented, which reflects this broader approach and is designed to facilitate a *comprehensive* test for both tool using and tool making, as more of the fossil record is revealed.

#### RECENT APPROACHES

Since humans can make stone tools with an ape-like power grip, should we abandon the hypothesis that the human hand evolved in adaptation to tool behaviors, and the expectation that fossil hominid hand morphology will reflect stages in the evolution of tool behaviors? Rather than rejecting the notion, we need to abandon untested assumptions of links between hand morphology, precision gripping, and tool making, and to test whether the hominid hand evolved in adaptation to *economical and effective* manipulation of tools. Currently three areas of investigation are providing insights into possible links between several types of precision gripping, hand morphology, and effective tool behaviors. These are: (1) the experimental replication of prehis-

toric stone tools by humans; (2) the systematic comparative study of precision gripping in humans and other catarrhine species; and (3) the biomechanical analysis of hands in humans and nonhuman species.

#### Precision grips actually used in the manufacture of prehistoric stone tools

How does one perform the experiments and make the evaluations in the absence of living representatives of prehistoric hominids? Three indirect approaches provide clues to the minimal requirements of hand morphology for effective precision manipulation of the tools, and to features that enhance the behaviors. These are (1) the experimental replication of prehistoric stone tools by archaeologists (Marzke and Shackley, 1986), (2) observation of stone tool making by contemporary groups that still use stone tools (Toth et al., 1992), and (3) the experimental replication of prehistoric stone tools by our close pongid relatives (Schick and Toth, 1993; Toth et al., 1993).

**Experiments in the manufacture of stone tools.** Marzke and Shackley (1986) found that the replication and use of Oldowan tools elicited primarily three grips: the pad-to-side grip between the thumb and the side of the index finger, the 3-jaw chuck ("baseball") grip, and the cradle precision pinch grip by the thumb and four finger pads (see Figs. 1 and 2). Strong pinch as well as precision handling of stones by the thumb pad and the side of the index finger (with and without buttressing by the other fingers) were effective for cutting with flakes against strong resistance, and also (with buttressing) for stabilizing stone preforms in one hand against blows by a hammerstone in the other. The 3-jaw chuck pinch grip with precision handling is the most effective one for throwing, and for the strong pinch and precision maneuvering of round hammerstones when they are used to remove flakes from stone cores. The cradle pinch and handling grip occurred frequently when firm pinch and maneuvering of large stone preforms by the thumb and four fingers of one hand were required during flake removal by hammerstones. The grip involves extensive movement of the thumb in

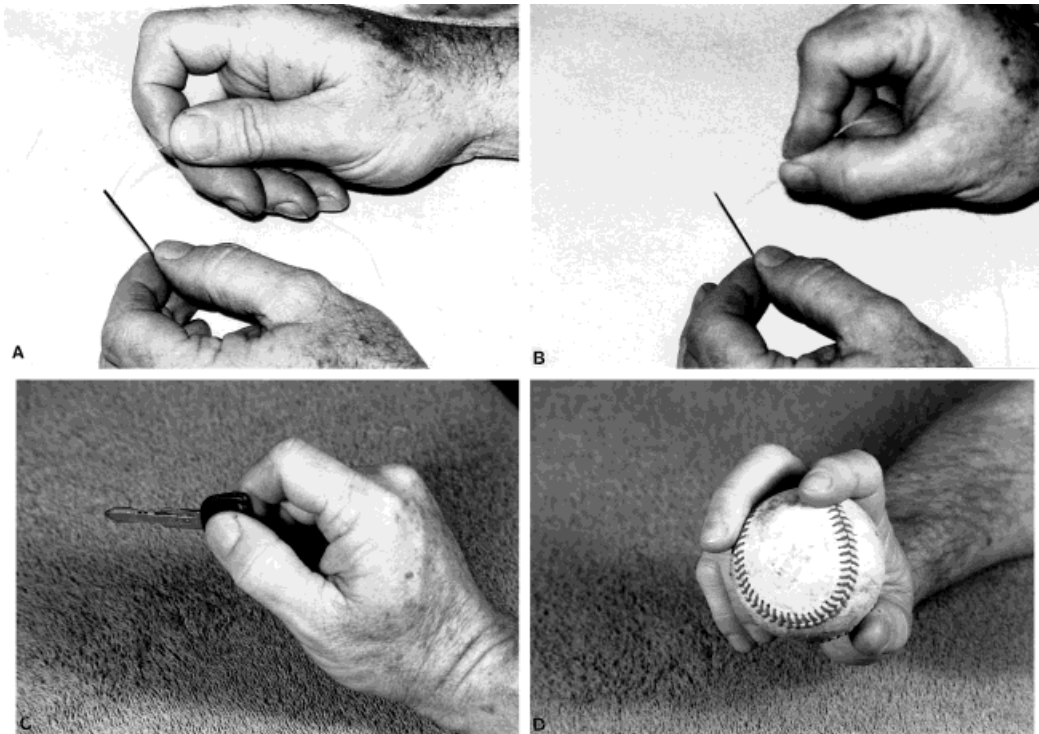


Fig. 1. Human precision finger grips. **A:** Two-jaw tip-to-tip. **B:** Two-jaw pad-to-pad. **C:** Two-jaw pad-to-side. **D:** Three-jaw full finger pad-to-pad ("baseball").

opposition to all four fingers. All these grips provided the extensive contact surfaces on the hand needed to control large preforms or hammerstones *by one hand alone*. The facility for generating a strong precision pinch provides the ability to expose a greater surface of a stone than would be possible if the stones were embedded in the palm and fingers in power grips. The exposed surface can be struck by the hammerstone or used in pounding and digging without injuring the fingers.

The same grips were again prominent during a recent experiment in which hand muscle recruitment during stone tool use and tool making was monitored with electromyography, during simultaneous videotaping of the hands (Marzke et al., abstract submitted). Especially striking was the constant repositioning of the stone core by the thumb and fingers of the non-dominant hand, in preparation for each strike of the hammerstone by the dominant hand. This precision

handling allowed for rapid core reduction. If a thumbless power grip of the core is used, the core must be repositioned for each strike either by dropping it and retrieving it in a new orientation or by shifting its position with the hand holding the hammerstone. There is savings in time and effort by precision handling.

These three grips have not extensively been discussed in connection with fossil hominids. The 2-jaw pad-to-pad precision hold of small objects was not recruited in these activities. Nor were power grips, which actively incorporate the palm. This latter observation seems curious in the light of experiments in stone tool making by Krantz (1960) and Napier (1962b, 1964), in which they showed that some tools could be made using the power grip exclusively. However, the purpose of their experiments was to determine whether these tools *could* be made without a well-developed human thumb, because the authors thought at the time

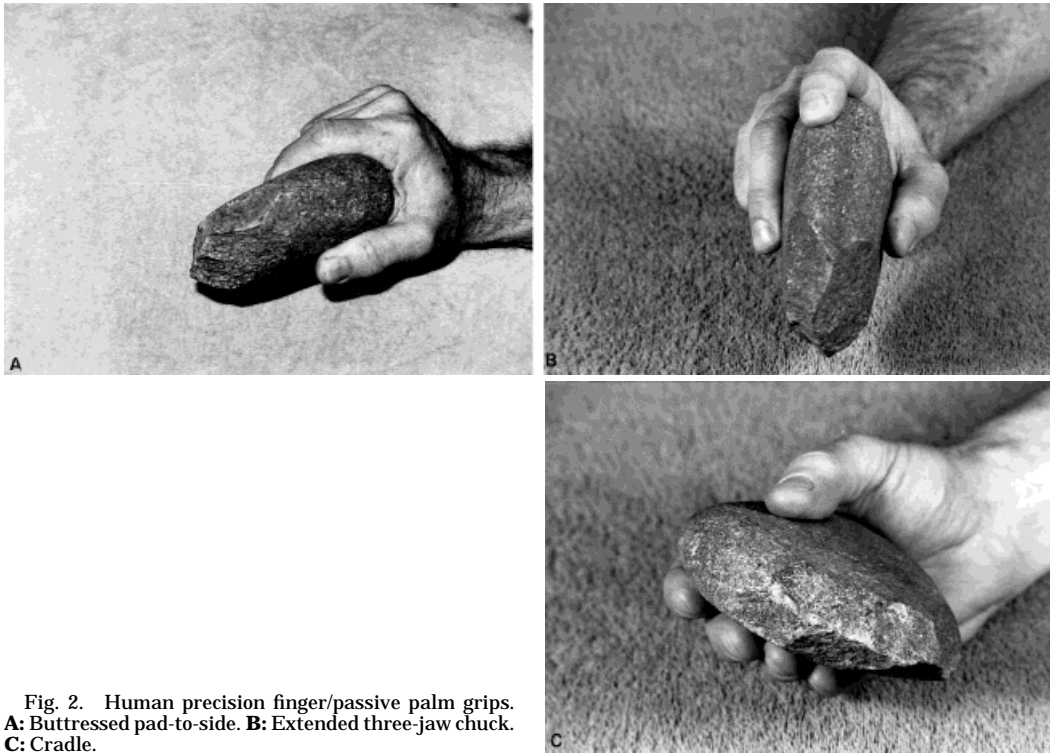


Fig. 2. Human precision finger/passive palm grips. **A:** Buttressed pad-to-side. **B:** Extended three-jaw chuck. **C:** Cradle.

that early hominid morphology facilitated only ape-like power grips. This was similar to asking whether this paragraph could be typed by the fifth finger. Certainly the potential is there, but the paragraph is more effectively generated, with less expended energy and less repetitive stress on a single joint, by ten well-trained fingers including the thumb. Our experiments with tool manufacture suggest that stone tool use is so greatly facilitated by capabilities for applying firm precision pinch grips as opposed to power grips, that only with the former capability would tool making have become *habitual*. Thus the results of the Napier and Krantz experiments were interesting, but not in the end relevant.

My collaborative work has led me to view the evolution of the human hand from a different perspective. Enormous advantages to tool use and tool making are provided by *modern* human hand morphology. From this vantage point, we may determine which elements of our grip repertoire, with their morphological underpinnings, are *essential*

to the efficient manufacture of stone tools comparable to those found in the prehistoric record. By observing archaeologists engaged in the manufacture of prehistoric tools we can evaluate the grips which have proved to be most effective in providing control, precision, and a minimum of injury and stress on the bones and joints. We found (Marzke and Shackley, 1986; Marzke et al., abstract submitted) that only the three precision grips listed above (along with precision handling), and no power grips, consistently expedite tool use and tool making with relatively little muscle fatigue and discomfort in the hand joints. This strongly implies that certain distinctive human features of the hand might reasonably be explained as adaptations to increasing demands for these precision grips with the evolution of prehistoric tools.

An objection to this line of reasoning has been raised by Sarmiento (1994), who states that "Because tools are fashioned to fit the hand that makes them, it is difficult, if not illogical, to interpret the anatomical struc-

ture of the human hand as adaptive to tool use." We disagree. For at least 2.5 million years the irregularly shaped raw materials used to fashion tools were held and wielded directly by hominid hands. The varied uses of these raw materials stressed the joints of the hands, and could *not* have been executed habitually and expeditiously unless the joints increasingly possessed ranges of movement, and constraints on mobility that assured effective grips with minimal repetitive stress and joint loading. We argue that our hand must have evolved first in adaptation to using these raw materials effectively, then to making tools and to using them habitually for a variety of manipulative activities that would have been impossible without evolutionary adaptations in bone and joint morphology to the stresses involved.

**Contemporary stone tool-making behavior.** Videotapes of hafted stone axe manufacture by a New Guinea group studied by Toth et al. (1992) reveal the same emphasis as our experiments, on cradle, 3-jaw chuck, and pad-to-side grips. They also reveal an absence of thumb pad/index finger pad grips, during the removal of flakes from the stone axe preforms. It is not until the stage at which the axes are hafted by the New Guinea tool-makers, by pinching fiber with the thumb and finger pads and winding it around the axe and its handle, that the latter grip is recruited.

**Nonhuman primate stone tool-making behavior.** A bonobo ("Kanzi"), trained to remove flakes from stone cores with a hammerstone, has demonstrated that human-like hands are not necessary for this activity (Schick and Toth, 1993; Toth et al., 1993). However, he developed another technique for flake removal on his own which has become his favorite (Schick and Toth, 1993). The technique is to throw stones forcefully with one hand against a hard tile floor, or against a cobble on the ground. It achieves flake removal without requiring control of a stone by one hand against external forces. Toth et al. (1993) found that the impact forces between the stones were much larger in throwing against the cobble than those the chimpanzee was capable of producing

using a hammerstone. This finding further highlights the importance of focusing on *forceful, one-handed* manipulation of stones in tracing the morphological basis of hominid tool making.

### Precision gripping in chimpanzees and hamadryas baboons

Prehistoric stone tool manipulation does not necessarily elicit the much-discussed thumb pad-to-index pad grip (Marzke and Shackley, 1986), but instead involves a number of precision grips that are both dynamic and forceful, and are not frequently described in the literature on human and nonhuman manipulative behavior. We initiated observations of manipulative behavior in several nonhuman primate species. Circumstances under which precision grips are elicited were recorded, grips were categorized according to the positions of the thumb and fingers, and it was noted whether the grips involve maneuvering of objects by the thumb and fingers, or forceful holding of objects against resistance.

**Chimpanzees.** Marzke and Wullstein (1996) observed five precision grips used by captive chimpanzees to retrieve and/or hold foods, tools, and other objects of various sizes by the thumb and fingers (Table 1). The most common of these were (1) a pad-to-side hold between the thumb and the side of the index finger and (2) a cup hold, in which an object is supported passively by the up-turned palm and propped by one or more fingers, held in parallel, and by the thumb, held at varying angles of opposition to the fingers. (This grip is distinguished from power grips by the lack of enclosure and squeezing of the object against the palm.) The chimpanzees also used holding grips between the thumb tip (not the pad) and the tip, distal pad, or dorsal aspect of a finger, for retrieving small objects (for example, the tip/tip hold during grooming). A grip between the full thumb and index finger pads was not observed. The pad-to-side grip was used for holding fruit rinds during feeding, for stripping leaves from stems, and for one-handed probing with or holding of objects against moderate resistance. When maintenance of the pad-to-side or cup hold

TABLE 1. Chimpanzee precision grips used for retrieval and holding of objects

Number of fingers ("jaws") in grip	Thumb/finger position	Thumb/finger/palm position
	<b>Precision finger grips</b>	<b>Precision finger/passive palm grips</b>
2-jaw chuck (thumb/index)	Tip-to-tip hold Pad-to-tip hold Pad-to-dorsal hold Pad-to-side hold	
3-5-jaw chuck (Thumb/2-4 fingers)		Cup hold (thumb/palmar surfaces of fingers; object rests against upturned metacarpals)

was threatened by external forces, such as pulling of citrus fruit pulp from the rind by the teeth, the other hand (and occasionally a foot as well) was recruited. It appears that the thumb and fingers together are not able to generate a firm enough balanced pinch to resist more than moderate forces dislodging the object. This finding is consistent with the behavior of the bonobo "Kanzi" during tool making. The chimpanzee thumb and fingers also do not precisely maneuver objects; changes in the orientation of an object are effected primarily by movements at the wrist and forearm joints, or by transferring the object to the lips and retrieving it again by the hand in the desired orientation.<sup>2</sup> A distinction is therefore made in the grip classifications of Tables 1 and 2, between the precision holding grips of chimpanzees and the precision pinch and handling grips of humans.

**Hamadryas baboons.** Guthrie (1991) and Jude (1993) reported for hamadryas baboons the pad-to-side and pad tip-to-pad tip holding grips described above for the chimpanzee as well as a pad-to-pad hold, in which both the thumb and index distal interphalangeal joints are extended to bring the volar pads over the distal phalanges into opposition. These grips were effective for

retrieving and holding food and other objects against mild resistance, but two hands (using the pad-to-side grip) were called into play when a more firm hold was required, as in breaking hard biscuits, for example. The thumb and index finger were not observed to precisely maneuver prehended objects.

The pad-to-pad hold has also been observed by Rose (1977) in olive baboons feeding in the wild and by Jolly (1970) in *Theropithecus gelada*. Napier (1961) noted that terrestrial cercopithecines in general closely approach humans in the capacity for this grip.

### ***Contrasts in precision gripping between humans and the two nonhuman species.***

Modern humans exhibit all the precision grips described above for retrieving and holding of small objects by chimpanzees and hamadryas baboons. They also use the pinch and handling grips listed in Table 2 and illustrated in Figures 1 and 2. The human precision gripping repertoire appears to be distinctive in three ways. First, humans often apply considerable force to these grips, achieving precision pinch as opposed to less firm precision holding. Landsmeer (1962) and others stress the delicacy of precision grips, but many of our modern tools also require a firm pinch (without a power squeeze by the palm) to meet resistance, as, for example, in our experimental stone tool making. Second, humans accommodate the thumb and fingers to the shape of objects, abducting and rotating the fingers to bring their volar pads into contact with the surface of the object, further enhancing security of the grip. This is seen, for example, in the 3-jaw chuck grip of hammerstones by the archaeologists in our experiments. Third, humans adjust the orientation of the object (i.e., they translate and rotate the object) through movements at the carpometacarpal, metacarpophalangeal and interphalangeal joints of the thumb and fingers, as described by Landsmeer's (1962) term "precision handling." These movements are fine-tuned by displacements in the cushion-like pads on the distal phalanges, and facilitate activities such as the rapid reorientation of stone cores for flaking by the archaeologists.

<sup>2</sup>These grips are also described and/or illustrated in recent studies by Christel (1993) and Boesch and Boesch (1993), which approach chimpanzee manipulative behavior from other perspectives and are discussed in Marzke and Wullstein (1996).

TABLE 2. Human precision grips for retrieval, holding, pinching, and handling of objects

Number of fingers in grip	Thumb/finger position	Thumb/finger movements
	<b>Precision finger pinch grips</b>	<b>Precision handling</b>
2-jaw chuck (thumb/index finger)	Tip-to-tip Pad-to-pad Pad-to-tip Pad-to-side	Tip/pad translation and pad/pad rotation
3-jaw chuck (thumb/index/medius)	Tip-to-tip Distal finger pad-to-pad Full finger pad-to-pad	Translation and rotation Tip/pad translation and pad/pad rotation Pad/pad rotation and translation
4- and 5-jaw chuck (thumb/fingers 2-4, 5)	Tip-to-tip Distal finger pad-to-pad Full finger pad-to-pad	Tip/pad translation and pad/pad rotation Pad/pad rotation and translation
	<b>Precision finger/passive palm pinch grips</b>	
2-jaw chuck	Buttressed pad-to-side (object rests on 2nd metacarpal; index finger buttressed by fingers 3-5; free thumb supplemented by 1st metacarpal)	Translation and rotation
3-jaw chuck	Extended 3-jaw chuck (object rests against 2nd metacarpal, buttressed by 1st metacarpal)	Pad/pad rotation and translation
4- and 5-jaw chuck	Cradle (thumb/palmar fingers with object resting against metacarpals)	Pad/pad rotation and translation

In my view the acme of human precision gripping is our ability for firm precision pinching of large objects by one hand, using the full or partial volar surfaces of the thumb and one or more fingers to secure the pinch and also to maneuver the object. This capacity represents a breakthrough in our evolution, enhancing tool using and facilitating stone tool making. The precision grips with these special capabilities are the buttressed pad-to-side, 3-jaw chuck, and cradle grips. The acme of chimpanzee precision gripping is their ability to effectively hold objects between the thumb and side of the index finger, while the acme of hamadryas baboon gripping is thumb pad/index finger distal pad holding.

I emphasize that the tool-making experiments by Marzke and Shackley (1986), which concentrated on the manufacture of Oldowan and Acheulean tools, did *not* elicit the grip requiring full opposition of the distal thumb and index pads exclusively. Experiments with Middle and Upper Paleolithic tools may identify activities in which this grip was used. Napier (1965) may have been correct when he suggested that our facility for this grip may not have evolved until the Upper Paleolithic.

**New classification of precision grips.** The classification of grips presented in Tables 1 and 2 is a natural extension of Napier's

classification. It also incorporates elements from Long (1981), Marzke and Shackley (1986), Shrewsbury and Sonek (1986), and this study. Grips are distinguished and defined on the basis of the postural and dynamic aspects of gripping and the segments of the hand involved. Thus the human ability to both pinch tightly and maneuver objects between the thumb and the side of the index finger is distinguished from the chimpanzee ability to hold objects with the same posture by the three terms "pad-to-side hold" (chimpanzee grip), "pad-to-side pinch" (human static grip), and "pad-to-side handling" (human dynamic grip).

The proposed classification for primatologists and paleoanthropologists is intended to serve as a vehicle for generating new insights into the behaviors and morphology that are distinctive of modern human manipulative skills in tool making. Detailed functional analysis of the grips in the new classification will allow us to deduce directly from fossil hands associated with these tools how the tools were made, and which species are likely to have made them.

#### **Morphology relating to precision gripping in humans, chimpanzees, and hamadryas baboons**

**Humans.** The following eight morphological features distinguish humans from other nonhuman primate species. Altogether they



form a pattern which is favorable to achieving the firm precision pinch grips and precision handling that in our experiments (Marzke and Shackley, 1996; Marzke et al., abstract submitted) appear to be essential to effective tool making. The features are described below, and our recent findings are incorporated under number 3.

1. Broad ungual tufts. Susman (1979) has shown that humans have proportionately broader tufts on the distal phalanges than apes. The tufts support pads whose large surfaces distribute pressure during forceful grasping and whose mobility allows accommodation of the pads to uneven surfaces as well as fine-tuning in the positioning of objects. The difference is illustrated in Shrewsbury and Johnson (1983, Fig. 1), who confirm Susman's observation. The large friction surface would have been essential for securing and controlling the cradle pinch of large preforms and the 3-jaw grip of hammerstones in habitual tool making.
2. A long thumb relative to the length of the fingers. Humans are distinctive among primates in having the longest thumb relative to the second finger (Napier, 1993). This is well illustrated in Schultz (1969). The distal pad of the thumb is therefore able to control objects of varied sizes and shapes against the volar aspects of extended or moderately flexed fingers during pinch and translation and rotation of the objects. A long thumb is important to prehistoric tool making because it can control stones with the volar aspect of extended or only partially flexed fingers on the opposite side of the stone. The longer the thumb relative to the fingers, the greater the control of the stone. Fully modern human thumb/finger proportions probably would have been essential only for tasks requiring firm pinch and precision handling of small tools by the thumb and the full pads of hyperextended distal phalanges.
3. Proportionately well-developed intrinsic muscles of the thumb. Tuttle (1969) found that the thumb intrinsic musculature constitutes 39% of total intrinsic hand musculature in humans, compared with

33% in hylobatids and 24% in chimpanzees and orangutans. Results of a recent comparative kinematic analysis of thumb muscles in a sample of 8 chimpanzees and in 2 samples of 7 humans each (Marzke et al., 1995; Marzke et al., in press) show that three of these muscles have a much greater potential in humans for stabilizing the thumb during strong pinch grips of objects. Applying techniques used at the Mayo Clinic for measuring muscle force potential and tendon moment arms (Chao et al., 1989; An et al., 1991; Linscheid et al., 1991; Horii et al., 1993), it was found that the human oblique adductor pollicis and opponens pollicis muscles have not only larger physiological cross-sectional areas (PCSA, a measure of potential force) but also larger tendon moment arms (MA) for flexion/extension at the carpometacarpal joint than are found in the chimpanzee sample (Table 3). It can be seen from Table 3 that the potential torque (PT, a product of PCSA and MA) is therefore approximately 15 times that of chimpanzees for the oblique adductor and almost triple the chimpanzee PT for the opponens. Also at the carpometacarpal joint the human flexor pollicis brevis MA for abduction/adduction is 4.7 times that of the chimpanzee sample. Since the PCSA is the same for the two species, humans have 4.7 times the PT in flexor pollicis brevis because of the difference in MA (Table 3). When human pinch grips concentrate opposing force at the ends of the digits, very large moments of stabilizing muscles are required at the proximal joints (Brand and Hollister, 1992). Thus, during the manufacture of stone tools, the more forceful the hammering, the more muscle torque is required to stabilize the proximal thumb joints in maintaining the pad-to-side, 3-jaw chuck, and cradle pinch grips of the stones. Our kinematic findings have pinpointed the joint regions and muscle attachment areas whose comparative biomechanical analysis will clarify details of joint function *relevant to the precision grips most*

TABLE 3. *Intrinsic thumb muscle mean physiological cross-sectional areas, tendon moment arms, and torque potential at the trapeziometacarpal joint, exhibiting marked differences between chimpanzee and human samples<sup>1</sup>*

Muscle	Activity	Species	PCSA (cm <sup>2</sup> )	MA (cm)	PT (cm <sup>3</sup> )
Adductor pollicis (oblique head)	Carpometacarpal flexion/ext.	Human	3.13	2.35	7.36
		Chimpanzee	1.25	0.38	0.48
Opponens pollicis	Carpometacarpal flexion/ext.	Human	2.63	1.25	3.29
		Chimpanzee	1.50	0.74	1.11
Flexor pollicis brevis (superficial head)	Carpometacarpal abduction./add.	Human	1.42	0.98	1.39
		Chimpanzee	1.42	0.21	0.30
	Metacarpophalangeal flexion/ext.	Human	1.42	0.63	0.89
		Chimpanzee	1.42	0.40	0.57
Adductor pollicis (transverse head)	Carpometacarpal abduction/add.	Human	0.89	1.66	1.48
		Chimpanzee	1.25	3.32	4.15

<sup>1</sup> Chimpanzee data are from a recent study by Marzke et al. (in press). The human moment arms are from a just-completed study at Mayo Clinic, Rochester, MN, kindly provided prior to publication by P. Smutz. Human PCSA data are from Linscheid et al. (1991). PCSA: physiological cross sectional area; MA: moment arm; PT: potential torque (PCSA × MA).

*likely to predict stone tool-making potential in fossil hominid hands.*

- Proportionately large flexor pollicis longus muscle. The PCSA of the human deep pollical flexor muscle constitutes approximately 22% of total thumb muscle PCSA (Table 4). The muscle has an origin on the radius which is usually independent of the origin of the deep flexor muscle to the index finger (Spinner, 1984). A large attachment area for its tendon may be seen on the volar aspect of the distal phalanx of the human thumb (Susman, 1979). The muscle is frequently absent in great apes (Straus, 1942). In most nonhuman primates with the muscle, it emanates from, or has a shunt with muscle fibers that contribute tendons to one or more fingers as well (Lewis, 1989; Tuttle, 1969, 1972; for comparative illustrations see Figures 7.3 and 7.4 in Lewis, 1989).

The fibers supplying the deep pollical flexor tendon generate flexion of the distal phalanx of the thumb, and thus are capable of maintaining both the orientation of its pad toward the fingers and its flexion against pressure by the fingers. Presence of the muscle does not necessarily reflect an emphasis on thumb pad/finger pad grips. An et al. (1983) found that the pad-to-side pinch grip elicits greater force by the muscle than tip-to-tip and pad-to-pad grips. The muscle is essential to precision handling, during which it functions with the long thumb extensor to move the interphalangeal joint as the prehended object is maneuvered by the distal thumb and finger pads. A possible

TABLE 4. *Mean physiological cross-sectional areas (PCSA) of thumb muscles in humans*

Muscle	PCSA (cm <sup>2</sup> ) <sup>1</sup>	Sample size
Flexor pollicis longus	5.1	4
Extensor pollicis longus	1.9	4
Abductor pollicis longus	3.9	4
Extensor pollicis brevis	1.3	4
Abductor pollicis brevis	1.6	7
Opponens pollicis	2.6	7
Flexor pollicis brevis (sum of superficial and deep heads)	2.3	7
Adductor pollicis (transverse)	0.9	7
Adductor pollicis (sum of 2 oblique heads)	3.1	7
Total PCSA	22.7	

PCSA data are from Chao et al. (1989, p. 44) for the first four muscles and from Linscheid et al. (1991, p. 276) for the remaining muscles.

alternative to the pinch function of the muscle in human ancestors could have been a chimpanzee-like flexion "set" of the distal pollical interphalangeal joint (see section on Chimpanzees below), which resists hyperextension of the distal pollical phalanx. Pinch force could have been achieved by contraction of well-developed intrinsic muscles. However, a separate deep pollical flexor has the advantage of facilitating both precision pinch and precision handling.

- Radial orientation of the third metacarpal head (Fig. 3). Susman (1979) found that the human third metacarpal head is distinctive among hominoids in its orientation toward the thumb. This orientation brings the palmar surface of the third proximal phalanx into opposition to the thumb with flexion (Susman, 1979),

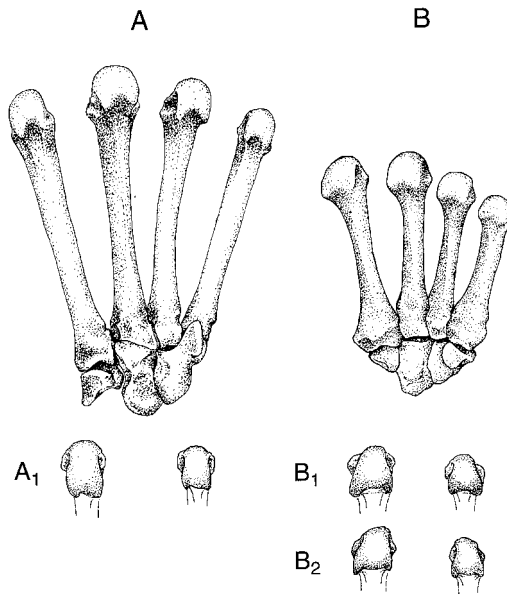


Fig. 3. Metacarpals 2-5 and proximal carpal row of the left hand, volar aspect, in a chimpanzee (A) and a human (B). Note in the human the radial orientation of the third metacarpal head. In the disto-volar view (1) of the second and fifth metacarpal heads, note in the human the marked volar cam on the radial aspect of the index metacarpal articular surface and on the ulnar aspect of the fifth metacarpal surface. The surfaces are also beveled dorsally on their outer margins. The cams and beveling may also be seen in the second and fifth metacarpals (A.L. 333-48 and A.L. 333-89) of *Australopithecus afarensis* (2). (Drawn from casts kindly provided by the Institute for Human Origins.)

maximizing the potential contact area between the volar skin of the fingers and thumb. The advantage of the orientation is particularly obvious for the 3-jaw chuck grip of stones in throwing and hammering.

6. Marked asymmetry of the second metacarpal and fifth metacarpal heads (Fig. 3). This feature was noted by Lewis (1977, 1989) in his comparison of humans with nonhuman primates. The radial side of the articular surface on the second metacarpal head bulges radially on its volar aspect and is beveled in an ulnar direction dorsally. This pattern is mirrored by the ulnar side of the articular surface on the fifth metacarpal head. The effect of the cam-like projection and dorsal beveling is to cause tension of the adjacent collateral ligament as the proximal phalanx is flexed, resulting in pronation of

the index finger and supination of the fifth finger. These movements thus bring the full palmar surfaces of the fingers into contact with the irregular surfaces of objects. The fingers may be accommodated to the shape of objects, and are able to rotate the objects through movements at the metacarpophalangeal joints. These movements are fundamental to the human potential for securing precision pinch grips and for performing precision handling of tools.

7. Orientation of the second metacarpal joints with the trapezium and capitate away from the sagittal plane (Figs. 4, 5). Marzke et al. (1992) found in 100% of a sample of 142 human hands that the joint between the second metacarpal and capitate was oriented distally, away from the sagittal plane, compared with a sagittal orientation in 100% of 59 nonhuman hominoid hands. The metacarpal joint with the trapezium was oriented between the coronal and transverse planes in 91% of 11 human hands, and sagittally in 95% of 57 nonhuman hominoid hands. The distal orientation of both joints in combination in humans has two important advantages. First, it allows pronation of the metacarpal during strong pinch between the thumb and the side of the index finger, and in the 3-jaw chuck grip. Second, it provides a proportionately larger surface area for distribution of axial load during use of these grips (Marzke, 1983; Marzke and Shackley, 1986). Both functions buffer the effects of repeated stress on cartilage lining the joint surfaces, associated with pronation of the finger and contraction of index finger musculature. These stresses are likely to have been considerable, particularly with the pad-to-side and buttressed pad-to-side forceful manipulation of stone preforms and flakes.
8. Spines on the ungual tufts. Shrewsbury and Johnson (1983) describe spines on the volar aspect of the distal phalanges which provide attachment to radial and ulnar tuberospinous ligaments. The ligaments support a proximal compartment of the pads, which is relatively mobile. There is also a distal compartment, with

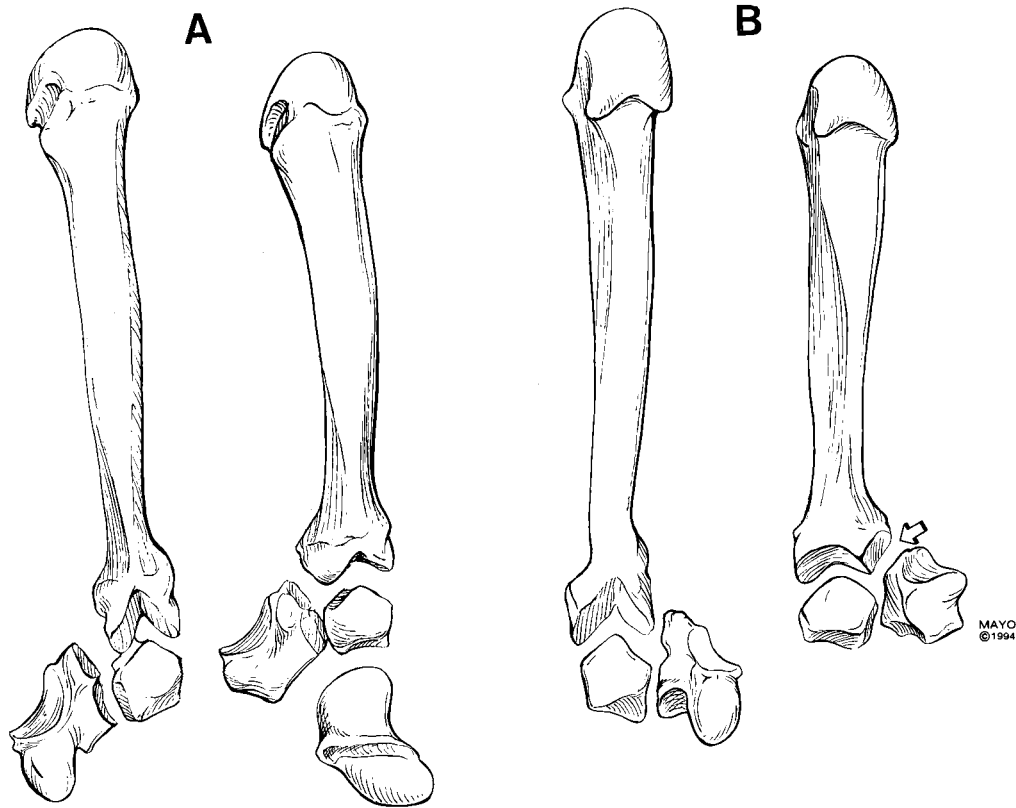


Fig. 4. Joints between the second metacarpal, trapezoid, and trapezium. **A:** Dorsal view of chimpanzee (left) and human (right). **B:** Volar view of chimpanzee (left) and human (right). Note in the human the volar-proximal orientation of the metacarpal joint surface for the trapezium (arrow).

a roughened volar surface on the ungual tuft reflecting the attachments of fascial fibers which restrict mobility of this compartment, thus reducing the amount of pinch pressure necessary to maintain hold of objects (Shrewsbury and Johnson, 1983; see especially Figs. 1, 2, 4, and 5). Comparative dissections and analyses of grips utilizing this region of the thumb and fingers by Shrewsbury and Sonek (1986) indicate that this compartmentalization of the tufts into a mobile proximal and a less mobile distal section is unique to humans, and that it permits a variety of precision postures (tip-to-tip, pad-to-pad, and pad-to-tip). These are capable of exploiting individually or in combination the firmness of pinch afforded by the distal compartment together with the cushioning, mobility, and larger sensory

area of the proximal compartment. While the features associated with compartmentalization may not be essential to firm precision grip and precision handling of stones, they probably would have enhanced these behaviors, since deformation of the compartmentalized pads allows finely controlled translation and rotation of stones. Their occurrence in fossils, together with other features essential to the behaviors, would be indicative of potentially very effective precision manipulation by the thumb and distal finger pads.

**Additional morphology claimed to be distinctive of humans.** Susman (1994) discussed another feature, a broad first metacarpal head relative to metacarpal length, which he considers to be distinctive of hu-



Fig. 5. Distal surface of the right capitate in a chimpanzee (left) and human (right). The facet for the third metacarpal occupies the entire surface in the chimpanzee, with the second metacarpal surface at approximately right angles to it on the radial side. In the human, the concave second metacarpal surface may be seen to the right of the third metacarpal surface, facing more distally than in the chimpanzee.

mans. He attributes the greater relative breadth in humans to the presence of three muscles (flexor pollicis longus, flexor pollicis brevis deep head, and a first palmar interosseus) that are lacking in chimpanzees, and suggests that human tool behavior explains the larger number of muscles. This reasoning is then applied to the functional interpretation of metacarpal head size in fossil hominid species; nonhuman manipulative behaviors are inferred from a narrow head in *A. afarensis* and human-like tool behaviors are inferred from a broader head in the Swartkrans fossils.

These hypothesized links between joint surface breadth, muscle number, and tool behavior are open to serious question. First, the joint surface breadth was compared only in humans and chimpanzees. Hamrick and Inouye (1995) and Ohman et al. (1995) applied Susman's measurement to gorilla thumb metacarpals, which proved to fall within the human range of variation. Second, the number of muscles is not in itself relevant to a comparative analysis of joint surface size relative to muscle function. What matters is the total amount of torque generated by muscles at the metacarpophalangeal joint. Third, the three human muscles

that are missing in chimpanzees cannot serve as predictors of human-like tool behavior, since they are also present in Old World monkeys. In these monkeys, fibers from the deep flexor muscle layer supply a tendon to the distal thumb phalanx (Marzke, 1971). The fibers are comparable to the human flexor pollicis longus fibers in their potential for generating distal phalangeal flexion and for contributing to internal stress on the thumb joints. Also a first palmar interosseous muscle is characteristic of Old World monkeys (Lewis, 1989) and so is a deep head of the flexor pollicis brevis muscle (Day and Napier, 1963; Lewis, 1989).

**Chimpanzees.** We were surprised to discover a set of three morphological features in chimpanzees that appear to be adaptations to their manipulative behavior, in a hand which is otherwise quite highly specialized in its long fingers and strong finger flexor musculature for suspensory behavior (Marzke et al., 1994). The features, which enhance their pad-to-side holding grip, include the following. First, a saddle surface for the metacarpal on the trapezium which is narrow and convex in its anteroposterior dimension, particularly on its ulnar aspect (Guthrie, 1991), so that during opposition of the thumb the proximal volar beak on the metacarpal rides up on the trapezial convex saddle, locking against it. This locking mechanism is capable of stabilizing the joint during pressure of the thumb tip against objects held along the side or volar aspect of the index finger, but it limits excursion of the metacarpal in opposition to the fourth and fifth fingers. Second, a distal interphalangeal joint of the thumb which generally cannot fully extend (Tuttle, 1969, 1970; Shrewsbury and Sonek, 1986; Marzke and Wullstein, 1996). The thumb is thus positioned in such a way that its tip is directed toward the index finger when an object is held between them. In humans, the flexor pollicis longus muscle, which is frequently absent in chimpanzees (Tuttle, 1970; Marzke, 1971), is a dynamic positioner of the distal phalanx. Third, the adductor pollicis muscle sends a tendon to the distal phalanx of the thumb. This tendon appears to function as a constraint on extension of the distal

phalanx. (This extra tendon has been observed in 16 of 18 chimpanzee cadavers in which the insertion was specifically examined during dissection in my laboratory, as well as in gorilla and orangutan specimens. It has also been reported by Tuttle, 1969, 1970.) In addition, the transverse portion of the adductor pollicis muscle has approximately three times the potential torque (PT) of the human muscle for thumb abduction/adduction at the trapeziometacarpal joint (Table 3; Marzke et al., in press).

The significance of our behavioral/morphological findings in chimpanzees to the investigation of prehistoric hominid manipulative behavior is that they reveal both a large repertoire of effective precision grips for retrieving and holding objects, with morphological correlates for one of them, and limitations on the forcefulness and maneuverability of these grips. These findings provide new morphological clues to possible manipulative adaptations in early fossil hominid hands, but they also put into relief the distinctive aspects of human precision gripping whose morphological correlates should also be sought in fossil hands.

***Hamadryas baboons.*** The morphological features of particular interest here are those facilitating the thumb pad-index finger distal pad grip, the so-called "acme" of human precision gripping stressed in the literature on hominid hand evolution. The features are built into a morphological pattern specialized (with relatively short phalanges) for semi-digitigrade locomotion. First, the index finger is particularly short relative to the thumb (Etter, 1973). Second, the distal interphalangeal joints are capable of extending fully and hyperextending, allowing much of the distal volar pad of the thumb to oppose its counterpart on the index finger (Jude, 1993). This pad-to-pad grip thus provides a relatively large surface area for maintaining hold of small objects. Third, as in the chimpanzee and humans, there is a saddle joint with incongruent surfaces (Rose, 1992) between the trapezium and first metacarpal, which allows the thumb pad to be brought into opposition to the pad of the index finger. Fourth, a tendon originating from the central fibers of the flexor digitorum profundus

muscle at the level of the wrist inserts into the base of the distal phalanx of the thumb, in a position to effect the application of pressure by the volar pad against the object held on the volar pad of the index finger.

These findings on hamadryas baboons return the thumb pad/index finger pad grip from the exclusive realm of "refined" human behavior to membership among grips merely shared with humans. Morphological correlates of the grip in the baboons should be considered among features that might have existed in the hominid ancestral hand prior to abandonment of quadrupedal locomotion.

### EVOLUTION OF THE HUMAN HAND, PRECISION GRIPPING, AND TOOL MAKING

In this section we consider how the information in Recent Approaches may be applied to the functional and behavioral interpretation of fossil hominid hand morphology.

#### Predictions from the comparative hominoid studies

The human morphological features described in Recent Approaches are significant in their combined ability to facilitate firm pinch and precision handling of stones by each hand alone. This ability is likely to have become essential to hominids when they grew increasingly dependent upon tools manufactured by the removal of flakes from core preforms. It is predicted that the features will appear in the fossil record when the prehistoric record indicates a trend from opportunistic flake production toward habitual, widespread and systematic Oldowan tool making. One would then expect to find skeletal evidence for the following: (1) thumb sufficiently long relative to finger length to permit pinch and maneuvering of stone cores, hammerstones, and flakes, (2) intrinsic muscle torque potential sufficient to maintain the pinch of these stones against strong resistance, (3) metacarpophalangeal joint surfaces allowing some degree of cupping by the fingers, and (4) broad distal phalanges which could distribute the load associated with strong pinch grips. None of these features in isolation would be sufficient evidence for tool making.

Note that it is likely that most of the morphological features that facilitate firm precision pinch grips, and perhaps even precision handling, evolved before the advent of stone tool making with increasing dependence upon the use of unmodified stone, bone, and wood tools. The effectiveness of activities such as probing, digging, nut-cracking, cutting, and throwing with these tools would have increased with the ability to orient the tools precisely and to hold them firmly in one hand against resistance. Therefore, caution is urged in attempting to distinguish an advanced stage of tool using from an early stage of tool-making capabilities among fossil hands. Presence of these features in fossil species permits confidence in their potential for habitual, effective tool making, but the features do not necessarily confirm that the species were tool-makers.

#### Stages in the evolution of tool behavior

What constitutes evidence of adaptations to tool behavior in fossil hominid hands? I define four stages through which tool behavior may have progressed. Stage 1 consists of occasional use and modification of natural objects for tools, with moderate control by hands specialized primarily for quadrupedal locomotor demands. This stage is illustrated by living chimpanzees, whose tool behaviors in the wild have been described by McGrew (1992) and by Boesch and Boesch (1993). With stage 2, there would have been increasing use of natural objects of various sizes and shapes as tools, facilitated by new, distinctively human morphologic features which increased pinch strength, finger control, and tolerance of new stresses associated with grips of the tools. Stage 3 manifests a dependence upon the manufacture as well as controlled use of unhafted stone tools. Stage 4 is characterized by the manufacture and use of hafted tools and very small tools, some of which probably required controlled pad-to-pad pinch by a thumb and index finger of human proportions.

#### Fossil evidence for stages in the evolution of precision grip capabilities and tool behaviors

**Stage 1.** It is likely that the ancestor we share with African apes would have had at

least the stage 1 capacities seen in chimpanzees for tool behavior. There is a set of morphological features in the chimpanzee thumb which are best explained by their frequent use of a pad-to-side precision holding grip (Marzke and Wullstein, 1996). The presence of these features in very early fossil hominid hand bones would suggest a similar precision holding specialization, and would predict potential for behaviors that exploit this gripping capability in chimpanzees.

**Stage 2: Hadar.** *Australopithecus afarensis* has three of the eight human features described in Recent Approaches, which should have facilitated two distinctively human precision grips (together with precision handling): the firm pad-to-side pinch and the 3-jaw chuck pinch. One of the human features (no. 6) is a cam-like projection on the volar radial side of the second metacarpal head and dorsal beveling of the articular surface (personal observation; Fig. 3), which would have caused pronation of the index finger as it flexed. This capacity was complemented by feature 7, which is orientation of the second metacarpal joints with the capitate and trapezium away from the sagittal plane. This orientation reflects a capacity for slight "give" of the metacarpal base in pronation. The features together allow for rotation of objects by the thumb and side of the index finger and for positioning of the full volar surface of the index finger on spherical objects to secure a 3-jaw chuck hold grip. The human orientation of the carpometacarpal joints also provides for accommodation of axial load, indicating that the joints may have been regularly sustaining strong index finger muscle contraction associated with a firm pad-to-side pinch of objects. The third feature is a longer thumb relative to the fingers than in chimpanzees (no. 2; Marzke, 1983). This should have provided an advantage in securing and controlling flakes with the middle and distal segments of the flexed fingers in the pad-to-side grip, and in holding relatively large stones by the three-jaw chuck grip. The thumb probably was not long enough to facilitate pad-to-pad precision pinch and handling of small tools by the thumb and distal finger pads. Cradle precision gripping by the

thumb and all four fingers of one hand may have been enhanced by a facility for supination at the fifth metacarpophalangeal joint. The fifth metacarpal head has an asymmetry that mirrors the pattern of the second metacarpal head (Fig. 3) and would have guided the proximal phalanx into supination with flexion. However, control of objects by this grip may have been limited by trapeziometacarpal morphology. The base of the thumb has a chimpanzee-like projecting volar first metacarpal beak, which probably stabilized pad-to-side grips but interfered with smooth excursion of the metacarpal in opposition to the fourth and fifth fingers, where it is needed to control large objects with the finger pads (Marzke, 1992).

Tool using by the thumb, index and third fingers would have been enhanced by the pad-to-side and 3-jaw chuck precision capabilities, but tool making would have been restricted by the limited potential for a firm precision cradle grip and precision handling with this grip. Pad-to-side pinch and precision handling may have been used to apply pressure to tools in activities such as cutting and probing or digging. The capacity for holding stones in a 3-jaw chuck grip would have been an advantage for stone-throwing (Marzke, 1983).

**Stage 2: Sterkfontein.** The fossils from this site have three of the human features listed in Recent Approaches, which would have facilitated at least the human pad-to-side precision pinch and handling grips. Ricklan (1987, 1990) describes a distal thumb phalanx (STW 294) which is broad (no. 1), with a tuft and spines reflecting compartmentalization of the pads (no. 8), and with dimensions and a tendon insertion mark indicating a well-developed flexor pollicis longus muscle with greater mechanical advantage than the human muscle. Information on features 2 and 5–7 is not available at present to indicate whether other precision grips involving the finger pads could have exploited these features of the thumb.

**Stage 2: Swartkrans.** Here human features of the thumb are found (nos. 1 and 4), which are compatible with a firm pad-to-side grip, but information is not available about

features associated with other precision grips. A distal thumb phalanx attributed to *Paranthropus* is described by Susman (1988b) as similar to that of modern humans in breadth (no. 1), reflecting a large overlying pad that would have facilitated firm pinch of objects against pressure by the fingers. It is also described as similar in the presence of an insertion area for the flexor pollicis longus muscle (no. 4). Susman is silent on the presence or absence of features that allow compartmentalization of the pulp on the broad distal phalanx (no. 8). He argues that a broad proximal joint surface, stout shape, and marked crest for attachment of the opponens pollicis muscle on a first metacarpal (SKX 5020), along with the broad pollical distal phalanx with an extensive fossa marking the insertion of the long flexor muscle, reflect a capacity for a precision grip comparable to that of modern humans (Susman, 1988b). None of these features, with the exception of pollical distal phalangeal breadth, has yet received the kind of systematic comparative analysis applied by Susman and by others to the 8 morphological features on which the present discussion is based.

There is no evidence in the available bones of morphology that might have limited 3-jaw chuck and cradle grip capabilities necessary for tool making. Information about morphological features that would confirm a potential for these grips and behaviors is unavailable.

A second thumb metacarpal (SK 84) has a marked volar projection of the articular surface on the head (Napier, 1959). Napier notes that the degree of projection is greater than he observed in his human and ape sample. It is likely to have provided an advantageous moment arm for metacarpophalangeal flexion/extension by the flexor pollicis brevis muscle. Since the muscle in humans has a larger moment arm compared with chimpanzees (Table 3), and plays an important role in stabilizing pinch grips involving the distal finger pads, the morphology of this Swartkrans metacarpal head has implications for precision grip potential in the species to which it belonged.<sup>3</sup>

<sup>3</sup>The SK 84 metacarpal has been attributed by Susman (1988b) to *Homo erectus*, rather than to *Paranthropus*, on the basis of a feature on the metacarpal head that he reports is shared with a



**Stage 2, or possibly 3: Olduvai.** Two distal finger phalanges attributed to *Homo habilis* at Olduvai have relatively broad ungual tufts (no. 1; Napier, 1962a,b; Susman and Creel, 1979), compatible with firm precision pinch and handling grips required for tool making, which involve the thumb and volar surfaces of the fingers. There is no evidence in other associated hand bones of limitations to these human precision grips required for tool making. The likelihood that the grips were possible is heightened by a broad metacarpal surface on the trapezium, which is significantly more flat than in modern humans (Trinkaus, 1989). This morphology suggests a potential for distribution of large internal forces (Trinkaus, 1989) associated with cradle, 3-jaw chuck, and pad-to-side pinch grips, as well as for extensive excursion of the metacarpal in opposition to all the fingers required for the cradle grip of large stones (Marzke and Shackley, 1986). Unfortunately the carpometacarpal and metacarpophalangeal joint regions of the four fingers are not preserved. Therefore whether their morphology would have permitted the cupping of the hand necessary to maximize contact of the volar surface of the phalanges with the large stones remains unknown.

The degree of precision handling facilitated by the broad distal pads may have been somewhat limited. Shrewsbury and Sonek (1986) concluded that features relat-

ing to compartmentalization of the distal phalangeal pulp (no. 8) are absent, indicating less differentiation of thumb/distal phalangeal grips than in modern humans.

Since the distal phalanx attributed by Napier (1962a,b) to the thumb may be a hallucial phalanx (Susman and Creel, 1979), it is not reasonable to consider the implications of its morphology for tool behavior.

## CONCLUSIONS

My analysis of precision gripping, tool behavior, and hand morphology leads to the following conclusions about morphological adaptations to tool behaviors.

1. *Flaws in recent inferences of thumb/distal finger pad precision gripping and tool making from morphology of the Olduvai and Swartkrans fossils.* A capacity for thumb/distal finger pad "fine" precision gripping cannot be inferred from the current supply of early hominid hand bones, because evidence is lacking for thumb/finger proportions. The link between early hominid hand morphology and this grip is somewhat misplaced in any case, because it has been demonstrated that effective Oldowan stone tool making does not require the grip.

An effort to identify a single morphological predictor of the thumb pad/distal finger pad grip (Susman, 1988a,b, 1989) is currently flawed by assumptions of links between joint size and number of muscles and between number of muscles and tool-making capacity. Many features must be considered, and to interpret them requires study of grips actually used in tool making and of relevant joint biomechanics.

2. *Precision grips essential to habitual and effective stone tool manipulation.* Experimental prehistoric tool replication consistently elicits three precision grips: the pad-to-side, 3-jaw chuck, and cradle grips. All three require the abilities to achieve firm pinch by each hand and to apply precision handling to the stones. Power grips are not appropriate for many tool-making tasks, because they expose the fingers to damage and prevent a continuous flow of flake removal from cores.

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thumb metacarpal found in association with the Nariokotome skeleton of *Homo erectus*, KNM-WT 15000. (This attribution is complicated by concern about attribution of the Nariokotome thumb metacarpal to *Homo erectus*, noted by Walker and Leakey, 1993.) Susman does not state whether the morphology of the Swartkrans metacarpal reflects a potential for precision gripping. Napier (1959) argued on the basis of evidence for considerable mobility at the proximal and distal joints of the metacarpal that the hand to which this metacarpal belonged might have been capable of tool using but possibly lacked the ability for precision gripping necessary for tool making. In his view this mobility was evidence that the thumb was shorter relative to the fingers than in humans, based upon his impression of an association between thumb mobility and relative length in apes. The mosaic nature of early hominid hand skeletons cautions against such an inference of hand proportions from joint morphology.

Susman (1988b) attributes a proximal phalanx from Swartkrans (SKX 27431) to *Homo habilis*. Its included angle of 34° sets it outside the 95% confidence limits of the human mean and within the confidence limits of means for gorillas and chimpanzees. Susman has not given a generic designation to the triquetrum, 2 metacarpals, 3 proximal phalanges, 3 middle phalanges, and 1 distal phalanx. He has not discussed the morphology of these bones in connection with the Olduvai bones attributed to *Homo habilis* (Susman and Creel, 1979), or with regard to implications for precision gripping.

3. *Precision gripping repertoires of humans, chimpanzees, and hamadryas baboons.* A variety of precision grip capabilities exists in all three groups. Humans share all the grips of the nonhuman groups, but their grip repertoire additionally displays: (1) firm precision pinch of objects by one hand and (2) precision handling of the objects by one hand. These are precisely the features of precision gripping required for habitual, effective stone tool making.
4. *Morphological features predictive of effective precision grip repertoires in humans, chimpanzees, and hamadryas baboons.* Eight features distinctive of humans are consistent with effective use of precision pinch and handling grips essential to tool making. These are broad ungual tufts, a longer thumb relative to finger length than in chimpanzees, strong intrinsic thumb musculature with large moment arms at the proximal joints, a well-developed flexor pollicis longus muscle, radial orientation of the third metacarpal head, marked asymmetry of the second and fifth metacarpal heads, orientation of the second metacarpal joints with the trapezium and capitate away from the sagittal plane, and spines on the ungual tufts associated with ligaments that compartmentalize the volar pads. Chimpanzees have a distinctive pattern of thumb morphology related to their pad-to-side holding grip by the short thumb and long fingers. A thumb pad-index finger pad grip in hamadryas baboons is dependent upon its short index finger relative to thumb length and distal index finger interphalangeal joint hyperextension.
5. *Morphology in fossils reflecting precision grip capabilities.* Morphological correlates to both human and chimpanzee precision grips are present in the hands of *Australopithecus afarensis*. The combined pattern suggests an ability to use some tools with greater force and finger control than can chimpanzees, but a limitation in thumb mobility for the making of stone tools. The Swartkrans hands have two human features in the thumb and the Sterkfontein hands have three, which are likely to have enhanced the

effectiveness of stone tool use. There is no existing evidence for limitations to tool-making capabilities, but these capabilities cannot be confirmed without additional positive evidence in the thumb and fingers. There is more compelling evidence for tool-making capacity in the Olduvai hand, but the potential range of effective precision grips and tool-making capacities cannot be confidently determined without specimens of finger metacarpal joint regions.

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